Disentangling weed diversity and weather impacts on long-term crop productivity in a wheat-legume rotation

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A B S T R A C T

Weeds can harm crop growth and yield by competing for light, water, and nutrients and can produce high global potential yield losses if not controlled. However, the effects of weed diversity have not been fully examined. Here, we have used long-term data (31 years) of a cereal–legume rotation from a locality in central Spain to determine the importance of internal and external (weather and weed diversity) factors on crop yield. We used a novel methodology based on dynamic systems to explore how weed diversity and weather factors interact with crop yields. The dynamic model used here integrated internal and external factors with additive or non-linear variants. We showed that internal processes (self-regulation) are involved in wheat and legume yield temporal fluctuations. The self-regulation of crop production appears to be stronger in cereal (85%) than in legume (45%) systems, and therefore legumes seem to be more sensitive to external variations. The legume crop was not affected by weed diversity but was instead negatively influenced by average temperature for the growing season. In wheat, there was a negative, non-linear response of yield to the interaction between richness and minimum temperature for the growing season. An improved understanding of the influence of weed diversity on crop yield may help to anticipate the effects of climate change and guide management practices to maintain crop productivity under sustainable agriculture.

1. Introduction

World population is expected to grow by over a third to reach 9 billion in 2050. This trend means that market demand for food will continue to grow. Agricultural production should increase by at least 50% before 2050 to support continued population growth and meet consumption trends (Alexandratos and Bruinsma, 2012). Crop yield dynamics are the result of the combined effect of internal (ecophysiological) and biophysical traits related to resource acquisition and use that can strongly limit the improvement of the basic functions of plants: growth, reproduction and survival, and the trade-offs between them (negative feedbacks which imply self-regulation) that constrain crop production and produced rapid and stable yield fluctuations) and external biotic and abiotic (e.g., climate perturbations) processes (Ferrero et al., 2014, 2018).

Competition from weeds is the most important external biotic factor out of all those that reduce crop yield (Oerke, 2006). Weeds can harm crop growth and yield by competing for light, water, and nutrients

(Zimdahl, 2007) and can produce high global potential losses if not controlled (Oerke, 2006). Estimated global crop losses to weeds are estimated in excess of $100 billion U.S. dollars (Appleby et al., 2000) and their control cost worldwide US $25 billion (Swanton et al., 2015). These data give an idea of the importance of understanding crop-weed interactions in order to develop a more sustainable agriculture.

Losses caused by weeds are often attributed to the impact of a few highly competitive weed species (Torner et al., 2006; Swanton et al., 2015), but a full appreciation of the effect of weeds on crop performance will result from a community-based approach. An increase in weed diversity can lead to a reduction in abundance of dominant, highly competitive weeds through an inter-specific competition effect and, consequently, a reduction in competitive pressure on the crop (Clements et al., 1994; Hooper et al., 2005). In this respect, differences in the competitive ability of each species within the weed community (Weaver and Ivany, 1998) and the small scale on which the competition takes place (Garrett and Dixon, 1998) could determine the intensity of competition with the crop. However, it has also been suggested that

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Table 1

Descriptive statistics for crop yield (kg/ha), precipitation (mm), temperature (degrees C) and weed diversity variables for wheat and legume production, 1985–2016. Mean growing-season (*pT*), mean last growing five months (*pT5*), maximum (*pMax*) and minimum (*pMin*) precipitation; minimum (*Tmin*), maximum (*Tmax*) and mean (*Tave*) temperature for the growing season, and weed community diversity indices : *Richness, Shannon and J-evenness.*

Variable	*Wheat* N = 156					*Legume* N = 156				
	Min	Max	M	SD	Md	Min	Max	M	SD	Md
Yield	384.10	7054.00	2457.46	1380.00	2402.20	525.70	10852.00	4766.43	2323.25	4469.20
Shannon	0.76	2.11	1.31	0.28	1.28	0.34	2.14	1.32	0.47	1.31
J-evenness	0.37	0.85	0.56	0.11	0.56	0.13	0.80	0.55	0.17	0.59
Richness	5	18	10.82	3.16	10	6	18	11.46	3.20	11
pT	219.10	528.60	370.42	99.56	335.20	185.80	524.50	396.42	95.08	376.70
pT5	52.30	325.80	174.62	73.13	178.50	55.10	186.60	109.30	35.95	104.40
pMax	57.50	179.90	107.28	31.04	99.10	0.10	16.00	6.35	5.63	4.70
pMin	0.00	26.90	5.96	6.99	5.40	95.80	363.10	232.22	71.17	218.30
Tave	9.60	12.51	10.77	0.81	10.76	8.41	12.04	10.83	1.08	10.87
Tmax	17.52	24.00	21.18	2.05	21.15	17.80	23.80	21.21	1.43	21.42
Tmin	1.90	6.56	4.41	1.29	4.37	1.70	8.00	4.49	1.61	4.20

Min, minimum; Max, maximum; M, mean; SD, standard deviation; Md, median; N, sample size.

increasing weed diversity could augment the probability of a highly competitive weed species being introduced into the system (Fargione and Tilman, 2005). There are few studies that relate weed diversity to crop performance and their results are contradictory. Ferrero et al. (2017) quantified a positive relationship between weed diversity and crop performance in soybean but a negative one in maize. Davis et al. (2005) found strong negative correlations of weed species density, species diversity, and total biomass with crop yield whereas other authors observed that an increase in species richness did not affect wheat yield (Pollnac et al., 2009). An improved understanding of the influence of weed diversity on crop yield may help in the design of cropping systems better able to drive more sustainable agriculture.

The objective of this study was to provide further insights into the link between weed diversity and crop performance in a wheat-legume crop rotation. We hypothesized the existence of an internal self-regulation process (based on negative feedback) regulating crop yield fluctuations and that increases in weed diversity would have a positive effect on wheat and legume productivity. Both hypotheses were evaluated with yield, weed density and weather time series data obtained from a 31-year long-term rotation and tillage systems trial in Spain, one of the oldest ongoing field experiments involving weeds. One advantage of long-term agricultural research is the potential to determine long-term trends in cropping system performance. For this purpose, we used an analytical tool that we have recently proposed based on dynamic of systems to investigate long-term crop yield fluctuations (Ferrero et al., 2014, 2017; 2018).

2. Material and methods

2.1. Study site and general experimental information

A 31 year time series of crop, weeds and site weather data were obtained from the El Encin Experimental Station (EES) (40° 29′N; 3° 22′W; Madrid, Spain, 610 m.s.l.). The soil is a Vertic Luvisol with a loam texture and 1% organic matter. The climate is semi-arid Mediterranean type (Strahler and Strahler, 1996), with hot, dry summers and mild, wet winters. Average annual rainfall during the 31-year study period was 430 mm (ranging from 230 to 765 mm). The average annual temperature was 13.8 °C (ranging from 11.9 to 15.5 °C). The experiment was initiated in 1985 and is ongoing. This paper refers to surveys conducted from 1985 to 2016 (missing data for 1990 and 1997). The cropping system consists of a 2-year winter wheat-legume (vetch or pea) rotation under three tillage treatments: conventional tillage (CT), minimum tillage (MT) and no tillage (NT). Tillage treatments were applied in a randomized block design replicated in 4 blocks (20 m x 30 m). Both crops were planted with a multi-purpose direct-drill machine with a

17 cm row spacing. Wheat planting date ranged from October 30th to December 19th. Fertilizers were applied at planting time (30 kg N, 30 kg P, 30 kg Kha^{-1}) and at mid-tillering (53 kg Nha^{-1}). Post-emergence glyphosate (0.2 l a.i. ha − 1 ioxinil + 0.2 l a.i. ha − 1 bromoxinil + 1.0 l a.i. ha − 1 mecoprop) was applied at the mid-tillering stage. Wheat harvest dates ranged from June 16 to July 14. Leguminous crops were planted between November 6th and January 19th. Average rates of fertilizer were 14 kg N, 14 kg P$_2$O$_5$ and 14 kg K$_2$O ha^{-1} for vetch and 19 kg N, 38 kg P$_2$O$_5$ and 71 kg K$_2$O ha^{-1} for pea and no post-emergence herbicides were applied. CT involved at least one mouldboard ploughing operation with a working depth of 25 cm, followed by a secondary tillage operation with a field cultivator (10–15 cm working depth). MT involved a primary cultivation with either a chisel plow or a field cultivator, followed by one secondary operation with field cultivator. In no-tillage, the only operation conducted prior to wheat planting was the application of glyphosate© 4–6 days in advance of planting (0.9 l a.i. ha − 1). When sowing leguminous crops in the NT treatment, straw and stubble from the previous wheat crop were destroyed by chopping with either the combine harvester at the harvest moment or the multi-purpose chopper prior to planting in both cases applying non-selective herbicide (e.g., glyphosate) thereafter.

Weed species abundance was recorded annually except in 1990 and 1997. Sampling took place in every experimental unit from February to April, depending on the crop maturation stage, and always took place before herbicide application. In the first three years of the experiment, five samples (30 × 33 cm) were taken per plot. Thereafter, 10 samples were taken except in 1995 when the number was 20 samples. Samples were collected along an M-shape pattern at intervals of approximately 15 m and 3 m away from field borders. The density (plants/m^2) recorded for each species in each of the samples was used to calculate three indices of the diversity of the weed communities: Richness, Shannon–Wiener and *J-evenness* (Table 1). Crop yields (*kg/ha*) were determined annually by harvesting each block (Table 1). A total of 44 weed species, typical of weed flora of central Spain arable fields, were found. *Papaver rhoeas, Veronica hederifolia,* and *Descurainia sophia* were the most abundant dicotyledonous species, whereas annual ryegrass (Lolium rigidum) was the most abundant grass (Hernandez Plaza et al., 2011). A previous study in the same place (Hernandez Plaza et al., 2011) showed that weed diversity was not influenced by tillage intensity. Therefore, data were pooled by crop before further analysis.

2.2. Weather-related variables

Meteorological data were obtained from the weather station located at the EES. Measures of precipitation included annual mean (*pT*), mean of the last five months growing-season (*pT5*), maximum (*pMax*) and
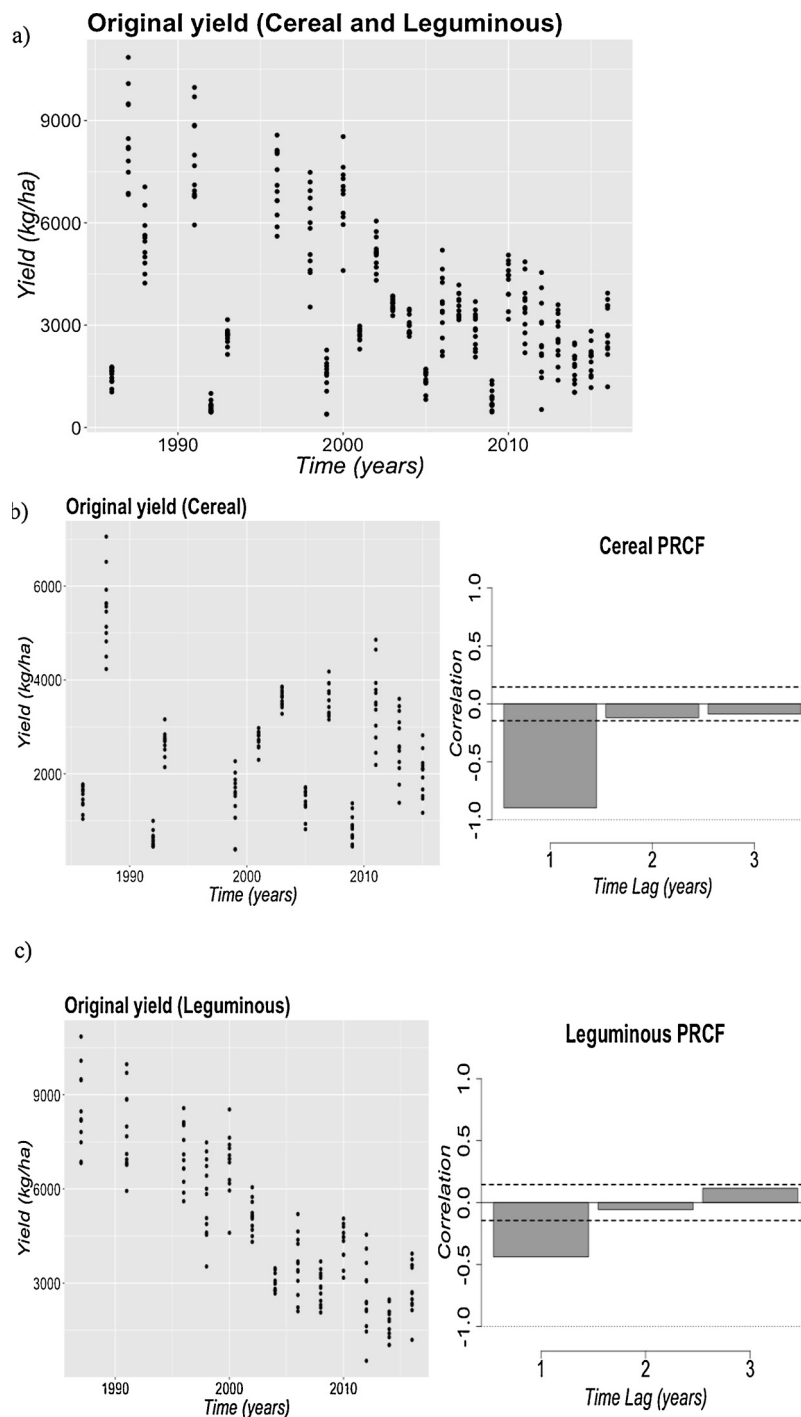
Fig. 1. Diagnostic tools for the log-transformed time series: a) Original time series b) original time series of cereal yields and c) original time series of leguminous yields, and Partial Rate Correlation Functions (PRCF).

minimum *(pMin)*. Measures of temperature included minimum *(Tmin)*, maximum *(Tmax)* and mean *(Tave)* values for the growing season (Table S1).

2.3. Diagnosis and yield dynamics models

Our statistical modelling approach has been described in detail in a previous publication (Ferrero et al., 2017). The analyses began with the generation of a stationary time series from the raw data (Fig. 1a).

To do this, we de-trended the data (i.e., rotating the series around the linear trend). Next, we defined the annual rate of yield increases as

$R_t = log\ Y_t - log\ Y_{t-1}$ (Lobell et al., 2011; Rosana et al., 2017) where Y_t is the de-trended yield at time t and Y_{t-1} is the same series with one year of delay (lags 1). R_t dynamics result from the combined effect of internal (crop biophysical adjustments by negative feedbacks) and external (e.g. weed diversity and weather perturbations) processes (Berryman, 1999; Lima et al., 2012; Ferrero et al., 2014, 2017, 2018). We built a set of models that included the result of the combined effect of both factors (Ferrero et al., 2014). The first model incorporated the effects of internal processes on R_t without any external perturbation. We used the generalized exponential form of the discrete logistic model (Ricker, 1954; *endogenous* model),

$$R_t = r_{max} - exp(a*Y_{t-d} + c) \tag{1}$$

where Y represents the log-yield data at time t and d is number of time lags to be included in the model, r_{max} is a positive constant representing the maximum productive rate estimated as the maximum value observed from the data, c is a measure of the ratio between supply and demand of limiting resources and a is shape parameter representing the non-linear interaction strengths. Partial rate correlation function (*PRCF*; Berryman and Turchin, 2001) was used to determine how many time lags (*d*) should be included in model 1. This function is flexible enough to detect a wide range of system behaviours and includes a biologically realistic property: the crop performance is bounded (Royama, 1992), because no crop can produce an infinite yield value, there must be an upper bound in R_t in Eq. (1).

Eq. (1) was modified to represent external perturbations (weed diversity and weather) (Lima et al., 2012; Ferrero et al., 2014). External (additive) perturbations were considered through the inclusion of the Z_t term,

$$R_t = r_{max} - exp(a*Y_{t-d} + c) + b*logZ_t \tag{2}$$

where Z_t is the external perturbation (weed diversity or weather conditions) and b is a parameter. Variation in Z_t modifies the equilibrium point and could alter its stability (vertical effect, *sensu* Royama, 1992; Figure S2).

Changes in c (Eq. (1)), imply external factors that act non-additively interactive effects of external perturbations (*lateral* effect, *sensu* Royama, 1992),

$$R_t = r_{max} - exp(a*Y_{t-d} + c + b*logZ_t) \tag{3}$$

Following Royama (1992) external perturbations affect R_t but not its stability (Figure S2).

Finally, external perturbations may have a complex influence on R_t dynamics as the nonlinear parameter, a, changes (Eq. (1)) (*nonlinear* effect, *sensu* Royama, 1992),

$$R_t = r_{max} - exp((a + b*logZ_t)*Y_{t-d} + c) \tag{4}$$

In this last case, both the equilibrium point and its stability could change (Royama, 1992; Figure S2). We included the combined effects and non-independence of predictors by including interaction terms in each of these models ($b*log(ZC_t/ZW_t)$); where ZC consider weather variables and ZW weed diversity.

2.4. Model fitting and model selection

Models 1–4 were fitted using nonlinear least squares regressions with the *nls* library in R software (R Development Core Team, 2016). A model selection criterion was used to rank competing models and to weigh the relative support for each one using Akaike weights (w_i) (Burnham and Anderson, 2003; Johnson and Omland, 2004) and the pseudo R^2 measures based on the deviance residual (Cameron and Windmeijer, 1996). We reported, the smallest subset of candidate models for which the w_i sum to 0.99.

3. Results

Our results highlight the importance of self-regulation in both the cereal and legume crop rotation phases through a first order negative feedback ($d = 1$) (PRCF(1); Fig. 1b,c).

The negative feedback generated result in stable first-order high frequency able to persist over time in a state of dynamics equilibrium with their environment (Ferrero et al., 2014). As a consequence of this stabilizing feedback, both crops exhibited stable approaches to equilibrium (regular oscillations). Biophysical internal processes contributed more to the wheat's dynamic ($R^2 = 0.83$; endogenous model in Table 2) than the legumes ($R^2 = 0.45$; endogenous model in Table 2).

Four plausible models for wheat and three plausible models for

legume were selected (Table 2, Figure S1). The pure endogenous model explained 45% of the R_t increase (endogenous model; Table 2) in legume. All the models selected included the effect of average temperature for the growing season on R_t which improved the explained variance of the pure endogenous model by up to 16% (Table 2). The results showed that the legume was affected negatively by average temperature non-additively (the best model: Eq. (3); $R^2 = 0.54$; $AIC_c = 5.62$; $w_i = 0.91$; Table 2; Fig. 2a) but was not influenced by weed diversity. Therefore, temperature affected legume yield potential, but not its stability, through changes in the amplitude or period of oscillation.

For wheat, all models slightly improved upon the pure endogenous model (Table 2), adding up to 4% of the additional variance explained. These models included negative effects from growing season's minimum temperature through interaction with weed diversity (richness and Shannon index) on R_t (Table 2). The best model (Eq. (4); $R^2 = 0.87$; $AIC_c = 182.48$; $w_i = 0.48$) included a non-linear response mediated by the interaction between minimum temperature for the growing season and richness (2). Therefore, the effect of minimum temperature on R_t was mediated by the weed richness. Following this model, both the equilibrium point and its stability could change.

4. Discussion

This study demonstrated that both internal and external processes contributed to yield fluctuations over time in winter wheat and legumes, A nonlinear first-order negative feedback structure captured the essential elements of both crop dynamics and indicated the existence of a rapid negative feedback, which tends to stabilize their dynamics over time (Berryman, 1999). Most of the literature points to external factors as being the exclusive drivers when explaining crop dynamics (Ray et al., 2015; Teasdale and Cavigelli, 2017). However, our results suggest that the endogenous feedback structure of the system should also be considered in order to fully understand crop fluctuations and in accordance with results obtained in other crops (Ferrero et al., 2014, 2017, 2018). Therefore, there is biophysical adjustments by negative feedbacks where the crop response (crop yield) is confined within limits because internal constraints determined by the crop genetic composition and the environment. Recent works have also indicated the necessity of recognising biophysical limits to crop yield in order to account crop yield growth and stagnation (Ray et al., 2012; Grassini et al., 2013). Individual physiology or height-structured competition for light affect the conversion of those resources into biomass (Purves and Pacala, 2008), so that crop yield growth rate is usually lower for high yield values.

In our study, the self-regulation in crop production was stronger in cereal (83%) than legume (46%). This discrepancy suggests that legumes are more sensitive to external factors. Cereals and legumes belong to C3 and C4-type plants, respectively. The latter being more influenced by temperature (Epstein et al., 2002). This circumstance could explain the difference in the strength of the self-regulation in both crops.

It is well known that weed infestations reduce crop performance (Swanton et al., 2015). In cereal crops, yield reduction due to weed interference is mostly caused by a few highly competitive weed species, such as winter wild oat (*Avena sterilis*) (Gonzalez-Andujar and Saavedra, 2003) which causes great damage in wheat (Barroso et al., 2011). However, there is little information in the literature, and it is mostly discrepant in respect of weed diversity affecting crop yield. Mohler (2001) predicted that more diverse weed communities should have greater potential to negatively affect crop yields because of the increased chance that one or more members of the community would be able to survive a given control measure. However, Ferrero et al. (2017) found a positive association between weed diversity and soybean yield and Pollnac et al. (2009) observed that an increase in species richness did not affect wheat yield. Our results indicated that the relationship between weed diversity and wheat is more complex than one might

Table 2

Selected crop yield models for wheat and legume production using the exponential form of logistic growth. r_{max} maximum finite reproductive rate, a non-linearity coefficient (non-linear model), c the ratio between demand and offer of limiting resources (lateral model); with b coefficients for different external effects, AIC_c corrected Akaike information criterion and w_i Akaike weights of a set of selected models, and R^2 pseudo-coefficient of determination. Tmin: Minimum temperature (ºC) for the growing season. Tave: Average temperature (ºC) for the growing season. Weed diversity indices (Shannon; Richness).

Crop	Model	Variable/s	r_{max}	a	c	b	AIC_c	w_i	R^2
Wheat	**No Linear**	**Tmin/Richness**	**2.04**	**0.87**[***]	**−0.03**[***]	**-6.36**[**]	**182.48**	**0.48**	**0.87**
	No Linear	Tmin/Shannon	2.04	0.97[***]	−0.03[***]	−6.61[***]	187.87	0.03	0.86
	Vertical	Tmin/Shannon	2.04	0.93[***]	−6.29[***]	−0.24[***]	187.25	0.04	0.86
	Vertical	Tmin/Richness	2.04	0.90[***]	−0.27[***]	−6.61[***]	182.63	0.44	0.86
	Endogenous		2.04	0.94[***]	−6.67[***]		217.05	0.00	0.83
Legume	**Lateral**	**Tave**	**0.71**	**0.37**[***]	**0.96**[***]	**−2.05**[***]	**5.62**	**0.91**	**0.54**
	Vertical	Tave	0.71	1.53[***]	−1.52[***]	−9.73[***]	11.82	0.04	0.52
	No Lineal	Tave	0.71	1.96[***]	−0.18[***]	−13.32[***]	11.62	0.04	0.52
	Endogenous		0.71	1.34[***]	−11.68[***]		28.94	0.00	0.45

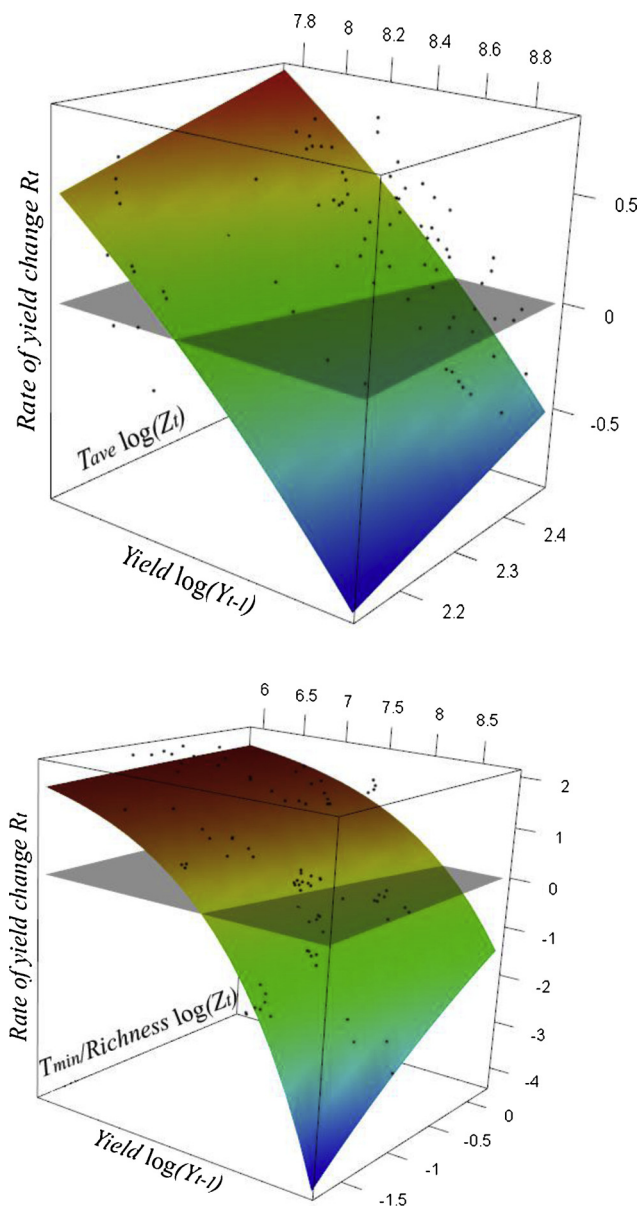In bold the best models for wheat and legume. **p < 0.01, ***p < 0.001.

Fig. 2. Crop yield rates of change R_t against the log observed yield level Y_{t-1} (with 1 year of delay) for: a) legume and b) cereal.

think at first glance and cannot be reflected adequately by the common weed-crop interference models (Zimdahl, 2007). Here we did not observe any direct effect of diversity on wheat, but rather a non-additive effect of richness and the minimum temperature for the growing season (Table 2). These results might explain why Pollnac et al. (2009) did not find an additive relationship between richness and wheat yield. The importance of the minimum temperature on wheat yield has been emphasized by different authors (Lobell and Ortiz-Monasterio, 2007; Duncan et al., 2015). Minimum temperature affects the anthesis and grain-filling of wheat crop development and this effect seems be mediated by weed diversity (richness) in a nonlinear way following our results. This implies that the effects of these variables should be considered in conjunction with constraints on the yield potential of wheat. The combined effect of minimum temperature and weed richness seems complex and requires further research. A possible hypothesis could be that the negative impacts of minimum temperature decrease with increasing levels of weed diversity (richness). Weed biomass or cover ratio can alter the wheat canopy microclimate in many ways (e.g. light interception) (Han et al., 2013). So, weed diversity might increase soil or canopy temperatures, favouring the crop's development. The non-linear effect and minimum temperature indicate that small changes in both variables could exert profound changes in wheat production.

The legume crop in this study was not affected by weed diversity but was instead influenced negatively by the growing season's average temperature. It is well documented that legumes are able to suppress annual weeds, for instance, during their early establishment phase (Dyck and Liebman, 1994). This circumstance could explain the lack of detection of any effect of weed diversity. Temperature is a major factor affecting seed yield and quality in legumes (Ruelland and Zachowski, 2010), because it affects many aspects of the N_2-fixation symbiosis, (e.g. inhibiting nodulation; Bordeleau and Prévost, 1994; Lira et al., 2005) Our model presents a negative effect of the growing season's average temperature on legume production which seems to explain the trend observed in Fig. 1. This is confirmed by the clear increment of the growing season's average temperature observed in the last ten years ($R^2 = 0.80$; P > 0.01) which could put in question the use of the rotation cereal-legume typical in the area.

The effect of temperature is though a lateral effect (sensu Royama, 1992; Figure S2) which implies an effect on the legume yield, in this case a negative one, but not its stability.

We have shown the existence of general patterns for wheat and legume yield dynamics based on the interactions between internal (biophysical limits by first-order negative feedback) and external (weather and weed diversity) factors. Deciphering the role of both factors could be important for guiding future weed management practices aimed to biodiversity conservation and provide ecosystem services. For instance, results of this study might benefit dry-land agriculture that could maintain certain levels of weed diversity without affecting crop performance and therefore, reducing the dependence of external inputs. On the other hand, our methodology could help to anticipate the effects of climate change, identifying those crops that are

most vulnerable (Ferrero et al., 2018)

Finally, we suggest the importance of dynamic models based in biological knowledge for understanding the interactions between weed communities and environmental factors in shaping the dynamic of crop yield.

Acknowledgements

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